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# BEHAVIOR AND ASSIMILATION

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## I

In a discussion of Liebig's law of the minimum (Hooker, '17), proof was given of the existence of an integrating principle which, as Adams ('18, p. 481) points out, is equivalent to Bancroft's law, so called because Bancroft ('11) was the first to indicate the application of Le Chatelier's theorem to biology. In fact, if it be admitted that organisms are systems in equilibrium, it follows that they obey the theorem of Le Chatelier. Bancroft's formulation of the law is "that a system tends to change so as to minimize an external disturbance." But this statement is so broad that it fails to convey the full significance of the theorem and apparently has led to some confusion. It therefore seems advisable to give a detailed discussion of the theorem of Le Chatelier in its application to biology and more particularly to point out its relation to other biological principles.

"It will be perceived," says Troland ('17, p. 325), "that the demand . . . is not for new biological facts, but for physico-chemical conceptions in terms of which a chaos of biological facts, already at hand, can be explained or systematized."

Findlay ('04, p. 56) defines the theorem of Le Chatelier as follows:

> *If a system in equilibrium is subjected to a constraint by which the equilibrium is shifted, a reaction takes place which opposes the constraint, i. e., one by which its effect is partially annulled.* . . . In all cases, whenever changes in the external condition of a system in equilibrium are produced, processes also occur within the system which tend to counteract the effect of the external changes.

Let us consider, by way of example, a simple case of a system of three phases, namely, ice, water and water-vapor, in equilibrium with respect to temperature and pressure. This system can exist only at 0° C. and at atmospheric pressure. If heat is withdrawn from the system and the pressure and volume are kept constant, a part of the water freezes to ice and the temperature is maintained by the latent heat of fusion. Since the formation of ice would increase the volume and therefore raise the pressure, a certain amount of vapor condenses to water. If heat is added to the system, changes take place in the reverse direction. Similar changes occur when the pressure is altered at constant temperature. In general (Findley, '04, pp. 56, 57), "so long as the three phases are present, no change in the temperature or pressure of the system can occur, but *only changes in the relative amounts of the phases;* that is to say, the effect on the system of change in the external conditions is opposed by the reactions or changes which take place within the system (p. 60). If the specific volumes of the phases are known and the sign of the heat effects which accompany the transformation of one phase into the other, it is possible to predict (by means of the theorem of Le Chatelier) the changes which will be produced in the system by alterations of the pressure and temperature. . . . It should be noted that *all three phases are involved in the change.*"

It is evident that these remarks apply in detail to the behavior of living organisms. The system in equilibrium is the organism. The external condition of the system is the environment. The constraint by which the equilibrium is shifted is the stimulus. The reaction that opposes the constraint and partially annuls its effect is the response of the irritable mechanism.

A stimulus is generally considered to be any change in the relation between the organism and a factor of its environment, but no response occurs unless the change be one by which the equilibrium is shifted, to effect which it must be, (*a*) of a magnitude sufficient to overcome the inertia of the system, that is it must be a liminal stimulus and (*b*) it must relate to a limiting factor of assimilation) cf. Hooker, '17, p. 204). Furthermore, the change in the relation between the organism and a factor of its environment may be produced either by a change in the environment, *i. e.,* it is heterotrophic, or by a change in the organism, *i. e.,* it is autotrophic, or by changes in both.

The response is characterized by the facts that (*a*) its nature and direction are determined by the stimulus but (*b*) the energy is supplied by processes that occur within the system; in other words the stimulus releases the response. Thus in the ice-water-vapor system when heat is withdrawn, this is supplied by the latent heat of fusion of ice. In this simple system there is a direct relation between the amount of heat withdrawn and the amount supplied. Such a relation does not exist in the behavior of organisms, nor should we expect it in such complicated systems. A wealth of examples illustrating the application of the theorem of Le Chatelier to the behavior of plants and animals will be found in Bancroft's article ('17). A brief discussion of the integrating character of development, evolution and biotic succession has been made elsewhere (Hooker, '17) and supplies illustrations of these principles. It will be sufficient to reiterate here that cells, organs and groups of organisms form systems as well as the single organism. Correlations and morphogenic responses are therefore conditioned in accordance with the theorem of Le Chatelier, and it is unnecessary to postulate the existence of hypothetical inhibiting substances to account for the normal behavior of parts.

Inasmuch as the reaction of a system is directed according to the theorem of Le Chatelier, every system in equilibrium is teleological. The means that produce the reaction are directed to a definite end, to overcome the constraint, and the reaction might be said to take place in order that the system may be preserved. This is evidently the source of the "purposefulness," that has occasioned endless biological discussion. The living organism, however, is teleological only to the same extent as the ice-water-vapor system.

These being the facts, the essential problem that confronts us is a study of the physical and chemical aspects of the equilibrium under the influence of a complex of environmental factors. There must exist some degree of correspondence between this equilibrium and the environment. Comparative morphological structure is evidence of this and the same must obtain of chemical composition. The task before us is not so much to ascertain the "function" of any particular substance or element, as to acquire a knowledge of the equilibrium as a whole, for it is only in relation to the other constituents that the function of any one compound can be understood. The need is consequently for a more detailed knowledge of the interrelationships of the chemical constituents and for determinations of how these relationships are altered by changes in the organism itself. This can probably be carried out more readily with plants, but the problem demands more comprehensive analyses than any that have hitherto been made. Investigations with these points in view are now under way and the remarks in this paper will serve as an introduction to them. A knowledge of the conditions governing the change from one phase to another within the organic system is a necessary prerequisite to a more complete understanding of organic equilibria. For the discussion of Le Chatelier's theorem has shown, that in any reaction all the phases are involved, and if the changes, such as the sign of the heat effects, etc., accompanying the transformation of one phase into another are known, it will be possible to predict by means of the theorem of Le Chatelier the effects that will be produced within the system by altering any of its relations with the environment.

Adams ('19, p. 74) says: "Irritability may not be causally explained, but it seems to obey these general laws in the same measure as causal changes." A complete description is the only adequate explanation. Although it is impossible to give a complete description of the physical and chemical processes involved in the irritable mechanism, it should be evident that organisms are irritable because they are systems in equilibrium and as such obey the theorem of Le Chatelier.

## II

When Adams ('18, p. 474) says, referring to Bancroft's law: "In other words this is a perpetuating tendency, a method of assimilation, of which reproduction may be considered but a special phase," he makes a serious error. That some other principle is involved is hinted at in the following passages (Adams, '18, p. 474, 475):

> In addition to influences which interfere with systems as expressed by Bancroft, there are those which reinforce or accelerate (tend to continue or hasten activity) and do not change its character, but only the intensity of the response (temperature, enzymes, repetition, etc.). By this method also systems tend to be perpetuated and organisms in "favorable" (non-interfering) conditions, tend to continue their normal activities.
>
> Thorndike in summarizing the laws of "acquired behavior or learning" formulates two laws. The first is essentially a statement of Bancroft's law of response to interference (discomfort or satisfaction) and the second (exercise or repetition) is that of reinforcement.

But when Adams ('18, p. 475) states: "This law appears to be a corollary of Bancroft's law which is concerned with interference or retardation," he is dodging the question.

The second principle which Adams calls the law of reinforcement is the basis of assimilation and the related processes of growth, reproduction and inheritance. That the assimilation of an organism may take place, three conditions are essential: (*a*) available materials to construct the organism; (*b*) a supply of energy; and (*c*) the presence of the living organism. There are also certain formal conditions of temperature, pressure, etc., which need not concern us at present. In short, assimilation is an autocatalytic process; because the end products of assimilation act as catalytic agents for their own synthesis. In green plants and the independent bacteria it is also an endothermic process, because the end products of assimilation have a higher energy content than the compounds from which they are constructed. As an illustration of an autocatalytic reaction between inorganic compounds, the formation of Millon's reagent may be cited. When mercury is dissolved in nitric acid, a certain amount of nitrous acid is formed. Nitrous acid is a catalytic agent for the solution of mercury in nitric acid, and therefore for its own production. To quote from Troland ('17, p. 337), who has discussed the theory of autocatalysis:

> The suggestion that the fundamental life-process of *growth* is the expression of an autocatalytic chemical reaction has been made independently by a number of investigators. It will be perceived that on the basis of the foregoing theory of autocatalysis, this suggestion becomes closely allied to the familiar and ancient comparison of vital growth to the growth of the crystal. The customary objection to this comparison, viz., that a crystal grows by accretion whereas protoplasm increases by intussusception, loses its force as soon as we regard living matter as a complex mixture of substances suspended by colloidal subdivision in water, since there is no evidence that the individual colloidal particles do not grow by accretion. On the contrary, it is almost inconceivable that these bodies, which are the real chemical units in protoplasm, should grow in any other way. The growth of a system like a cell could be regarded as the resultant effect of a very large number of component growths, each governed by its specific autocatalytic mechanism. It has been shown by T. B. Robertson that growth curves, with respect to time, actually do coincide in general form with the curve characteristic of an autocatalytic reaction.

In other words, the process of assimilation is like crystallization from a supersaturated solution by seeding with a crystal. The following quotation from Findlay ('04, pp. 67–68) throws light on this process:

> In general, then, we may say that a *new phase will not necessarily be formed immediately the system passes into such a condition that the existence of the phase is possible;* but rather, instead of the system undergoing transformation so as to pass into the more stable condition

> under the existing pressure and temperature, this transformation will be "suspended" or delayed, and the system will become metastable (that is temporarily stable as long as it is not brought in contact with the new phase). Only in the case of the formation of the liquid from the solid phase, in a one-component system, has this reluctance to form a new phase not been observed.
>
> *To ensure the formation of the new phase, it is necessary to have that phase present.* The presence of the solid phase will prevent the supercooling of the liquid.
>
> As to the amount of the new phase required to bring about the transformation of the metastable phase, quantitative measurements have been carried out only in the case of the initiation of crystallization in a supercooled liquid. As the result of these investigations, it was found that, in the case of superfused salol, the very small amount of $1 \times 10^{-1}$ gm. of the solid phase was sufficient to induce crystallization. Crystallization of the supercooled liquid, however, can be initiated only by a "nucleus" of the same substance in the solid state; . . . it is not brought about by the presence of any chance solid.

The following illustration is of interest in this connection. From a saturated solution of anhydrous sodium sulphate, $Na_2SO_4$, at 24° C. different compounds may be obtained by seeding with different crystals. If a crystal of the heptahydrate, $Na_2SO_4 \cdot 7H_2O$, is added, this salt crystallizes out; if a crystal of the decahydrate known as Glauber's salt, $Na_2SO_4 \cdot 10H_2O$, is added, Glauber's salt crystallizes out. In this case both the solution and the heptahydrate are metastable. It should be noted that the seeding accomplishes two things: (*a*) it induces crystallization and (*b*) determines the nature of the crystals. Moreover since the crystals produced are hydrates, they represent products of synthesis.

## III

Living organisms accordingly perform two processes, behavior and assimilation, and depending on whether the one or the other process is considered, they present fundamentally different aspects. If we make a cross-section (to borrow an expression of E. B. Holt) through the organism in one direction, it appears as a system in equilibrium obeying the theorem of Le Chatelier. If we make a cross-section at right angles, as it were, it appears as part of an autocatalytic reaction. Behavior and assimilation work in different planes. The theory of autocatalysis does not explain all biological enigmas as Troland ('17) intimates, nor does the theorem of Le Chatelier account for assimilation.

However, these planes intersect; the two processes are interrelated in the following four respects.

1. The factors of the environment that constitute the external conditions of the behaving system are the possible limiting factors of assimilation.
2. Assimilation is an endothermic process that supplies the energy expended by the responses of behavior.
3. Behavior overcomes the effects of the limiting factors of assimilation and so places the organism in what is, under the circumstances, the most favorable situation for assimilation.
4. Assimilation and growth eventually change the relations between the organism and the factors of its environment, consequently producing stimuli to behavior.

Behavior is the process by which the organism is able to cope with its environment, it renders its condition as "favorable" as the situation permits, but contributes nothing to its increase. It is the progressive element to which change and variability are due. It is the "guide of life." Assimilation is the autocatalytic process by which the organism increases and multiplies, but which would soon be brought to a standstill according to the law of the minimum, were it not for behavior. It is the conservative element that determines that like shall beget like; it is the principle of heredity. An organism may be defined as a system that perpetuates itself by autocatalysis and reacts according to the theorem of Le Chatelier.

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